8. DEEP-SEA ECHINODERMS IN THE TONGUE OF THE OCEAN, BAHAMA ISLANDS:

A SURVEY, USING THE RESEARCH SUBMERSIBLE ALVIN.

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SUMMARY

Deep-sea echinoderms of the Tongue of the Ocean, Bahama Islands, have been studied, using trawled collections made by the University of Miami together with observations from the deep submersible *Alvin*. Transect runs in the submersible permitted studies of population densities and behaviour of approximately 38 species of larger invertebrates, of which 27 were echinoderms. Several echinoderm species show a patchy distribution pattern which is apparently not related to available food resources. Some species are exclusively herbivores, feeding on fragments of turtle grass, *Thalassia testudinata* and sargassum weed, *Sargassum* spp. Feeding habits of some Tongue of the Ocean echinoderms are compared with those of the same species from further north, where supplies of plant material are not nearly so abundant.

Trawled collections of echinoderms do not include some of the most common and ecologically important holothurians; conversely, some burrowing species very common in the area were not observed from the *Alvin*. Further observations were made on swimming behaviour of holothurians. All swimming forms studied apparently derive nourishment from the seafloor. Short tracks on the seafloor indicate that swimming behaviour is a common means of transportation from one area to another. The ophiuroid *Bathypectinura heros* is capable of active swimming movements. Uniformly conical mounds on the seafloor are often built up around a central core of holothurian faeces.

INTRODUCTION

During January, 1977, a series of eight dives were made in the submersible D.S.R.V. *Alvin*, to depths in excess of 3,660 metres, in the Tongue of the Ocean, Bahama Islands. The purpose of the dives was to make ". . . first-hand observations . . on the biology of deepwater benthic fishes and larger invertebrates and to take qualitative and quantitative data by visual and photographic methods" (D. M. Cohen, 1 March 1977, Cruise Report NOAA — MUST dives with D.S.R.V. *Alvin* in the Bahamas — unpublished).

I was able to participate in four dives, and on one, Dive 703, an excellent opportunity was provided to make quantitative studies of echinoderms and other large invertebrates, and to observe activities of echinoderms. This paper represents for the most part the results obtained during Dive 703, although some aspects of "natural history" of echinoderms were obtained during one or more of the other dives in which I participated. Additional information on echinoderms from the Tongue of the Ocean was obtained from the extensive collections of the Rosenstiel School of Marine and Atmospheric Science, University of Miami, whose staff members have occupied numerous trawl stations in the Tongue of the Ocean over the past several years.

METHODS

1. LOCATION OF ALVIN DIVE 703 AND DESCRIPTION OF ACTIVITIES

Dive 703 was made on January 12, 1977 in the Tongue of the Ocean, Bahama Islands Australian Museum Memoir No. 16, 1982, 129-145 24°54.9'N, 77°41.1'W, at a depth of 1938-2141 metres. Total time on bottom 5.6 hours. Pilot, Dudley Foster, observers Daniel M. Cohen and David L. Pawson.

During Dive 703 a total of 11 measured transects were run. Transect 9 was aborted because of a malfunction in the metre wheel which was used to measure the distance traversed by the submersible. Transect runs were essentially consecutive, and were made in a south to south-easterly direction (see Table 1). Thus, no overlap of transect runs occurred.

Table 1. Transect runs covered by Alvin, Dive 703. Transect 9 was aborted due to equipment malfunction.

compass heading	distance run (m.)	area studied (m ²)
180	914	3,654
180	679	2,716
154	202	808
164	716	2,864
145	419	1,676
143	445	1,880
148	138	552
121	267	1,068
138	188	752
138	289	1,156
	4,257 metres	17,126 sq. metres
	180 154 164 145 143 148 121 138	$\begin{array}{cccccccccccccccccccccccccccccccccccc$

It has been estimated that an observer can see out for a distance of approximately 4 metres from the observer's viewing port in the pool of light thrown by the submersible's floodlamps. Knowing this distance, and knowing the distance traversed by the submersible during a transect run, it is possible to calculate the total area studied during a run, and then to determine the number of specimens of a particular species occurring per unit area. In the table shown here, population densities are expressed numbers of individuals per 1,000 m² (Table 2).

In order to estimate the accuracy of population counts made through the viewing port, a comparison was made between numbers of animals photographed in early transects by an E.G. & G. camera mounted on the submersible and numbers of animals counted, and results obtained were closely similar. A complete photographic survey for all transects was not possible because of the limited amount of film in the single camera.

The bottom was composed of a firm to flocculent greyish to light brown sediment, which contains very numerous pteropod mollusk shells of several species. Fragments of the floating alga, *Sargassum* spp., and roots and blades of turtle grass, *Thalassia testudinata* are ubiquitous on the seafloor (figs 1a, 1b). In a few areas they form mats, but for the most part the fragments seem to be more or less evenly scattered.

2. IDENTIFICATION OF ECHINODERMS VIEWED FROM ALVIN

Through the courtesy of Dr Gilbert L. Voss, I was able to examine the invertebrates collected by the Rosenstiel School of Marine and Atmospheric Science in the Tongue of the Ocean. This enabled a positive identification to be made of most of the echinoderms seen from the Alvin. Some systematic problems yet remain to be resolved.

Furthermore, the opportunity was taken to investigate stomach contents of selected species of ophiuroids and echinoids, so that feeding propensities could be determined. The University of Miami collections also included specimens of echinoderm species which are apparently common in the study area but were not observed during Alvin Dive 703. These taxa are

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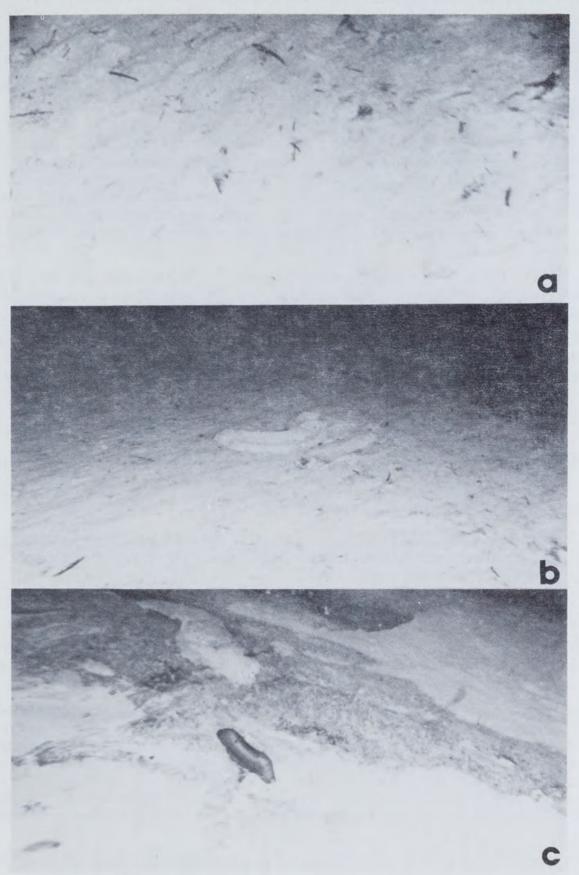


Fig. 1. Seafloor features. 1a, scattered fragments of *Thalassia* and *Sargassum* spp. Photo: D. M. Cohen. 1b, short track left by swimming holothurian, *Benthodytes*. 1c, *Benthodytes lingua* near rock outcrop.

discussed below.

RESULTS AND DISCUSSION

1. SPECIES STUDIED

During the ten successful transect runs, counts were made of 38 species of larger invertebrates. These comprise one sponge (Euplectella suberea Thomson, included in Table 2 for purposes of comparison of population densities), four coelenterates ("pennatulacean", Cerianthus sp., Anthomastus .sp. and Umbellula sp.), three crustaceans (Glyphocrangon sp., penaeid shrimp — Hepomadus sp.?, hemit crab), one pycnogonid (Colossendeis colossea Wilson), and two mollusks (white gastropod and octopus). The remaining 27 species were echinoderms, as follows—

ECHINOIDEA: Hygrosoma petersi (Agassiz), Phormosoma placenta Thomson, Plesiodiadema antillarum (Agassiz), Salenocidaris profundi (Duncan), Brissopsis elongata Mortensen, dead tests.

HOLOTHUROIDEA: Ellipinion delagei (Herouard), Benthodytes typica Théel, Benthodytes sanguinolenta Théel, Benthodytes lingua Perrier, Psychropotes depressa (Théel), Enypniastes eximia Théel, Deima validum Théel, Pseudostichopus species A, Pseudostichopus species B, Mesothuria verrilli (Théel), Paelopatides sp.

ASTEROIDEA: Nymphaster arenatus (Perrier), Ceramaster grenadensis (Perrier), Zoroaster fulgens (Thomson), Freyella species A, Freyella species B, "Luidia".

OPHIUROIDEA: Bathypectinura heros (Lyman), Ophiomusium species A, Ophiomusium species B, "red ophiuroid".

CRINOIDEA: "ten-armed sea lily".

A few other species of echinoderms were seen but not counted. These included numerous specimens of small pink ophiuroids (Family Ophiacanthidae?) clinging to sponges and small rocks, and pinkish five-armed euryalid ophiuroids, also clinging to sponges.

2. COMMON TONGUE OF THE OCEAN ECHINODERMS NOT COLLECTED BY THE UNIVERSITY OF MIAMI

The following species of holothurians are common in the area studied, but are not represented in the University of Miami collections: *Ellipinion delagei* (Herouard); *Enypniastes eximia* Théel; *Paelopatides* sp.

The first and last species were found to be numerically dominant in some transects (see Table 2). These species were not collected in trawls because they are exceedingly fragile and would be reduced to gelatinous masses in trawl samples. Furthermore, they are barely negatively buoyant, and are easily dislodged by the bow wave of the submersible; the bow wave of a trawl would have the same effect, materially reducing the possibilities of capturing specimens of these species. These species are highly important elements in the benthic biota of the area and their influence upon the composition and structure of sediments is undoubtedly important.

3. COMMON TONGUE OF THE OCEAN ECHINODERMS COLLECTED BY THE UNIVERSITY OF MIAMI, BUT NOT OBSERVED FROM THE ALVIN.

The following species of holothurians are common in the area studied, but were not observed during Alvin transects: Molpadia barbouri Deichmann; Molpadia musculus Risso;

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	Ophiuroidea 1. Bathypectinura heros 2/3. Ophiomusium sp. A/B 4. Red ophiuroid	Asteroidea 1. Nymphaster arenatus 2. Zoroaster fulgens 3. Ceramaster grenadensis 4. Freyella sp. A (6 arms) 5. Freyella sp. B (11 arms) 6. "Luidia"	Echinoidea 1. Hygrosoma petersi 2. Plesiodiadema antillarum 3. Phormosoma placenta 4. Salenocidaris profundi 5. Brissopsis elongata (dead)	Holothuroidea 1. Ellipinion delagei 2/3. Benthodytes typica/sanguino 4. Psychropotes depressa 5. Benthodytes lingua 6. Enypniastes eximia 7. Deima validum	8. Mesothurna verrilti 9/10. Pseudostichopus A/B 11. Paelopatides sp.	Crinoidea 1. Ten-armed sea lily Porifera (sponges) 1. Euplectella suberea

Gephyrothuria glauca (Clark).

The three holothurian species are apparently all burrowing forms. *Molpadia* species are known to be active burrowers (Clark, 1907; Rhoads and Young, 1971). It is surprising that *Gephyrothuria glauca*, with its dorsal whip-like papillae, is also apparently an infaunal species. It might have been expected that this species uses its papillae as sensory devices in a manner similar to that of the elasipodids, and that the animal is an epifaunal dweller.

Dead tests of the spatangoid echinoid *Brissopsis elongata* were observed during some transects (see Table 2); live specimens of this species were undoubtedly burrowed into the substratum in the same areas, but no trace of their burrows was visible from the *Alvin*.

It is evident from the above discussions that ecological studies of larger deep-sea invertebrates based entirely upon observations from submersibles or upon trawled samples might not necessarily reflect the true situation on the seafloor, and some of the most important "consumers" will be unwittingly omitted from consideration. It is important to remember that some of the most effective reworkers of sediments might not be represented in trawls or in photographs taken by submersibles.

4. INTESTINE CONTENTS OF SELECTED SPECIES

The intestine contents of several species of echinoderms collected in the Tongue of the Ocean by the University of Miami were examined, in order to determine which species might be using as food the fragments of seaweed and turtle grass that are scattered over the seafloor in that area. Vegetarian feeding habits are commonplace among the echinoids (Lawrence, 1975) but other echinoderms seem to be less inclined towards such a diet. In the case of two species of echinoids, comparisons were made with specimens collected from further north, where plant material is not nearly so abundant, but is nonetheless present, as Menzies et al. (1967) and Menzies and Rowe (1969) have shown for *Thalassia* and as Schoener and Rowe (1970) have shown for *Sargassum* spp.

a. Hygrosoma petersi: In all Tongue of the Ocean specimens examined, intestine contents consisted almost exclusively of fragments of Sargassum and fragments of Thalassia. Presence of occasional pteropod shells and foraminiferal skeletons indicate that some sediment is also ingested, but this may be accidental. Usually Sargassum dominated in intestines examined. Many Sargassum fragments carried colonies of encrusting bryozoans; apart from these, and the skeletal remains mentioned above, no other animal materials were found in the intestines. Specimens collected from further north (see Table 3), between Georgia and New York, appeared to have a more "mixed" diet, indicating that when abundant plant material is not available locally, this species can subsist on organic material extracted from sediments.

Mortensen (1935) studied specimens of this species from South Africa, West Indies and southwest Ireland, and found that the intestines contained ". . . only mud, formed into small balls about the size of peas." (p. 205). In a later paper, Mortensen (1938) noted that the Pacific species *Hygrosoma luculentum* (Agassiz) had its intestines filled with "bits of plants" (p. 226).

b. *Phormosoma placenta:* Intestine contents of this species in the Tongue of the Ocean consisted exclusively of small mud balls 1-3 mm in diameter, bound together by mucus. Several specimens from elsewhere in the Eastern Atlantic had similar mud balls in their intestines. This observation concurs with that of Mortensen (1935).

c. Plesiodiadema antillarum: Intestine contents poorly defined mud balls, not strongly bound by mucus. No plant material. Mortensen (1938, 1940) notes that P. indicum from the Indo-Pacific eats pieces of plants almost exclusively. Despite the abundance of plant material in the area, P. antillarum does not appear to ingest it.

Table 3. Size and intestine contents of Hygrosoma petersi from between Georgia and New York.	Iygrosoma petersi	from between Georgia and New York.
Albatross Station	Diameter of test (mm)	st Intestine contents
2678 32°40'N, 76° 40'30''W; 1,315 m	95 110 135, 145 150	mostly mudballs, 3 mm in diameter, also a few Sargassum fragments indeterminate plant and animal fragments Sargassum fragments and mud Sargassum fragments, some with encrusting bryozoans
2115 35°49'30'' N, 74° 34'45'' W; 1,517 m	155	unidentifiable weed fragments
2721 38°56' N, 72° 11′30′' W; 1,463 m	155	mostly mudballs 3 mm in diameter; few unidentifiable weed fragments
2181 39° 29'N, 71° 46'W; 1,258 m	150	Mudballs of various sizes, unidentifiable weed fragments
2691 39° 37'N, 71°08' W; 1,503 m	155	mostly Sargassum fragments with very few mudballs 3-4 mm in diameter.

d. Salenocidaris profundi: Intestine contents poorly defined mud balls; no plant material.

e. Ophiomusium spp.: The two species of Ophiomusium apparently consume nothing but sediment, perhaps on a non-selective basis. In most specimens examined the stomachs were virtually empty; in a few, the stomach was filled with sediment.

f. Bathypectinura heros: Of approximately 20 specimens examined, all but two had empty stomachs. The two exceptions contained exclusively fragments of Sargassum. Some of the "empty" stomachs contained a dark brown finely divided material that may once have been pieces of Sargassum. Madsen (1973) examined "a few stomach contents" (p. 142) of this species and found them to include mainly unidentifiable organic detritus, foraminiferans, etc. This then is the first record of a vegetarian diet in this species. Fell (1952) made the remarkable observation that the related shallow water New Zealand species Pectinura maculata (Verrill) can feed on anthers of the southern beech tree, Nothofagus sp., which fall into the water from overhanging trees. Schoener and Rowe (1970) found that another deep-sea ophiuroid, Amphiophiura bullata (Lyman), is capable of ingesting and presumably using as food bladders of Sargassum.

5. SOME ASPECTS OF BEHAVIOUR AND MORPHOLOGY OF SELECTED SPECIES

Hygrosoma petersi. This large, conspicuous and fast-moving epibenthic echinoid is common in several areas of the Atlantic Ocean in depths of 200-2,870 m (Mortensen, 1935). Grassle et al. (1975) note that the species is very active, and include an excellent photograph of a specimen in situ. Tongue of the Ocean representatives of this species differ in some respects from their conspecifics further to the north, which were observed by the author during *Alvin* Dive 592, at a depth of 1930-1988 m, in the area of Deepwater Dumpsite 106, 39°09.9'N, 71°54.8'W. The Tongue of the Ocean form has much smaller and less conspicuous hooves on the oral spines (see figs 2a, 2b), although in all other respects this form conforms to the traditional concept of the species.

These specimens also showed behavioural differences from the specimens observed during *Alvin* Dive 592. When being approached by the submersible, the northern specimens, upon sensing the bow wave (or the lights) would immediately "gallop" away from the source of the disturbance. The Tongue of the Ocean specimens were less inclined to move away rapidly; in many cases they remained in position, but directed their aboral spines away from the source of the disturbance.

Ellipinion delagei reached great population densities in some areas, especially during transect 7. This species is almost completely transparent when alive, and the body is virtually colourless. Through the body wall the coiled sediment- filled intestine can be clearly seen. Barham et al. (1967) and Pawson (1976) have found that some elasipodids tend to be oriented so that their anterior ends face into the prevailing current. In the case of *Ellipinion*, this tendency was exhibited to some extent, but was not rigidly followed. In some areas all specimens appeared to be facing in the same direction (fig. 2c), while in others a more random pattern of orientation was observed. In the study area there was almost no detectable current activity, and it is possible that in the absence of a significant current, the animals have a rather random orientation.

Benthodytes typica in the Tongue of the Ocean is generally light brownish to cream, with little evidence of shades of red. The anterior end is dark brown. This species was not observed to swim, not even when violently disturbed by the submersible's bow wave. A dense population of small (approximately 50 mm long) specimens was found in one area during transect 5. This might have been a year-class of specimens, leading to the suggestion that this species might have an annual reproductive cycle.

Benthodytes sanguinolenta is much more reddish than the preceding species, and usually

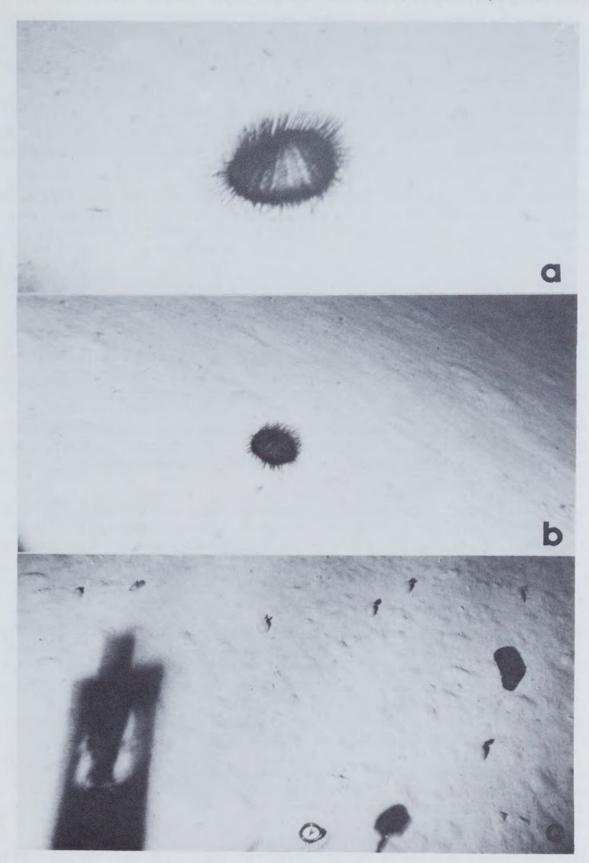


Fig. 2. Echinoids and holothurians. 2a, Hygrosoma petersi from Alvin Dive 592 (see text), with conspicuous hooves on oral spines. 2b, Hygrosoma petersi from Alvin Dive 703. Note that hooves are not visible, and that aboral spines are directed away from source of light (or from bow wave of submersible). 2c, six specimens of Ellipinion delagei, one of Benthodytes lingua (far right) and one of Psychropotes depressa (top left). Note that in this photo all specimens of Ellipinion are facing in the same direction.

considerably larger. Several specimens were observed to be swimming (figs 4a, b). Swimming movements were similar to those described for "Euphronides sp." (=Psychropotes depressa (Théel) according to Hansen (1975)) by Pawson (1976).

Benthodytes lingua is a large species, usually more than 30 cm long, uniformly light to dark violet (figs 1c, 2c). Specimens were relatively common in all transects and were among the most conspicuous invertebrates encountered during Dive 703. This species is apparently incapable of swimming.

Enypniastes eximia is common in the Tongue of the Ocean. The observations of Pawson (1976) can be enlarged upon here. Living specimens are light brown, translucent, and fragile. All but one of the specimens seen were swimming; some appeared to be drifting down towards the bottom passively, and others were ascending, gently undulating the anterodorsal veil. The mouth is apparently always directed upwards (figs 3a, b). All specimens observed swimming or floating past the viewing port were seen to have light coloured material of the same colour as the bottom sediments in their intestines. Eventually, a single specimen was found to be feeding on the seafloor (fig. 3c). The tentacles were very actively sweeping material in towards the mouth. We were unfortunately not able to determine the length of time that this specimen spent on the bottom, but judging by its active feeding rate, it would not need to remain there for more than a few minutes in order to fill its intestine. It seems likely that this species does rely on the seafloor for at least some of its food supply, and that it is not a permanent member of the nekton.

Paelopatides sp. was very common in some transects, especially numbers 5 through 8. Further identification of this species is impossible, regrettably, because the University of Miami collections did not include specimens of this fragile light pink species, which can reach a length of approximately 50 mm.

Pseudostichopus species A and B, and *Mesothuria verrilli* are often virtually indistinguishable through the viewing port of the submersible, because of their tendency to cover themselves with a layer of sediment (figs 4c, 5a). They were nowhere extremely common, but were conspicuous where they occurred because of their size (up to approximately 30 cm) and their conspicuous tracks. Systematic problems have necessitated a delay in making final identification of the two species of *Pseudostichopus*.

Freyella sp. is a six-armed brisingid asteroid which lies mouth down on the seafloor, with arms resting on the seafloor (Fig. 5c). This is an unusual feeding position for members of this family, for they usually raise their arms into the water column (Pequegnat et al., 1972, fig. W-1; Pawson, 1976, Pl. 3 figs. A-B). Maureen Downey of this Institution (personal communication) believes that this may be a new species of *Freyella*. A single specimen was collected by the *Alvin*, and it is now in the collections of the U.S. National Museum. The 11-armed *Freyella* sp. B was usually found on rocks, with its arms raised into the water column.

"Luidia" is a single specimen of five-armed asteroid which superficially resembled the genus Luidia. The arms were flattened, strap-like, and tapered gently from the small central disc to the bluntly pointed extremities. No specimens similar to this were found in the University of Miami collection.

Bathypectinura heros is a highly active uniformly orange ophiuroid, common in transects 1-4. It has been well described in two recent papers (Schoener, 1967; Madsen, 1973). Dr Daniel M. Cohen and I each saw a single individual of this species making active swimming movements in response to the approach of the submersible. In one case a specimen travelled a distance of approximately one metre by vigorously thrashing its arms. Maximum height above the seafloor was approximately one metre.

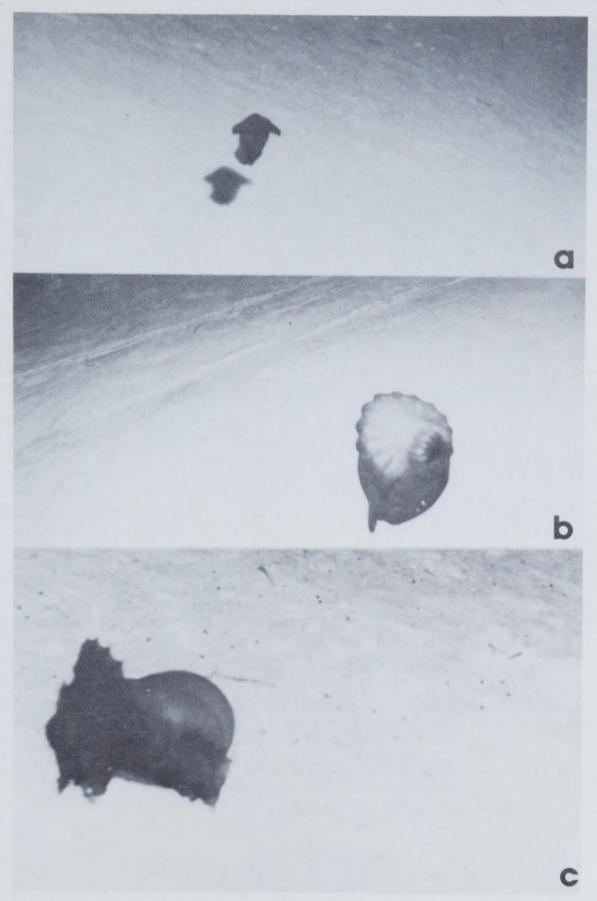


Fig. 3. The holothurian, *Enypniastes eximia*. 3a, specimen swimming, with gently undulating anterodorsal veil. 3b, another swimming specimen, showing mouth and tentacles. Photo, D. M. Cohen. 3c, a specimen on seafloor, actively feeding.

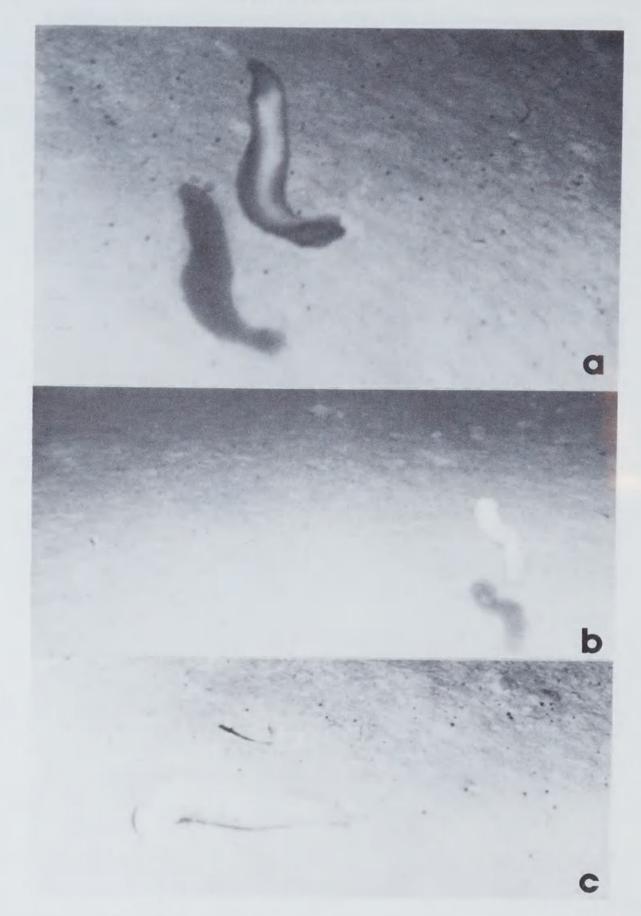


Fig. 4. Holothurians Benthodytes and Mesothuria. 4a, 4b, Benthodytes sanguinolenta swimming up and away from source of disturbance. 4c, Mesothuria verrilli on seafloor, with thin covering of sediment.

Ophiomusium species A and B have not yet been positively identified due to systematic problems. Barham et al. (1967), Grassle et al. (1975) and Wigley and Emery (1967) discuss behaviour and population densities of species of *Ophiomusium*.

"Red ophiuroid": this puzzling ophiuroid (fig. 5b) was seen in fairly large numbers during *Alvin* dives further north (see Cohen and Pawson, 1977). Regrettably, we were unable to collect any specimens of this brittle star. It is about the same size as *Ophiomusium lymani* with a light red disc, light orange-red arms and conspicuous red tube feet. Tongue of the Ocean specimens, like those observed further to the north, adopted a great variety of postures and also, presumably, feeding methods. Commonly, the animal lies mouth down on the seafloor with two or three arms raised into the water column. Several specimens were found occupying burrows (of their own making?) with two or three arms extended onto the seafloor surface. Others were more or less completely buried, with two or three arms projecting. A preliminary survey of University of Miami collections revealed no specimens which might represent this species, but a more detailed examination by a specialist is required.

6. FORMATION OF CONICAL MOUNDS ON THE SEAFLOOR

Several authors (Heezen and Hollister, 1971; Pequegnat et al., 1972, and others) have illustrated mounds of various kinds on the deep seafloor, and have suggested that the mounds are constructed by various burrowing organisms. It is well-known that some mounds with holes at their summits or with depressions near their bases are constructed by crustaceans or fishes. Other mounds, which are featureless, not associated obviously with other topographic features, have caused some puzzlement. During *Alvin* Dive 703 and other dives in the Tongue of the Ocean, several such mounds were disturbed mechanically by the movement of the submersible, and we were surprised to observe that in at least two cases the "core" of the mound consisted of a mass of holothurian faeces, such as may have been deposited by the genera *Ellipinion* or *Pseudostichopus*. Apparently the faeces, bound with some kind of mucus, act as a local surface feature upon which drifting and falling sediment can accumulate. In areas with little current activity, such mounds are almost perfectly symmetrical cones.

7. SHORT TRACKS ON THE SEAFLOOR

In numerous seafloor photographs, short holothurian tracks have been observed. These may begin and end within the field of the photograph, with no trace of the holothurian which made them. Two explanations may be offered to account for these tracks, and both involve swimming activities:

a. A swimming species landed on the seafloor, fed for a short distance, and then died, the dead animal eventually disappearing, leaving the track. Such a track may have been made very recently or perhaps hundreds of years ago, especially in areas were sedimentation rates are slow (Heezen and Hollister, 1971).

b. A swimming species landed on the seafloor, fed for a short distance, and then left again, perhaps to seek a more palatable sediment. During *Alvin* Dive 703, two specimens of *Benthodytes sanguinolenta* were seen to swim away, leaving short tracks behind them (fig. 1b). It is possible that a type of "trial and error" feeding is commonplace among the more mobile holothurians.

8. POPULATION DENSITIES OF ECHINODERMS

Counts of echinoderms in each transect (in numbers per 1000 m²) are given in Table 2. For comparison, counts for another large invertebrate, the Venus flower basket sponge *Euplectella* suberea Thomson are also given. Some comments on distribution patterns follow. In view of the large scale sized used, it is not considered profitable to submit the figures given here to statistical

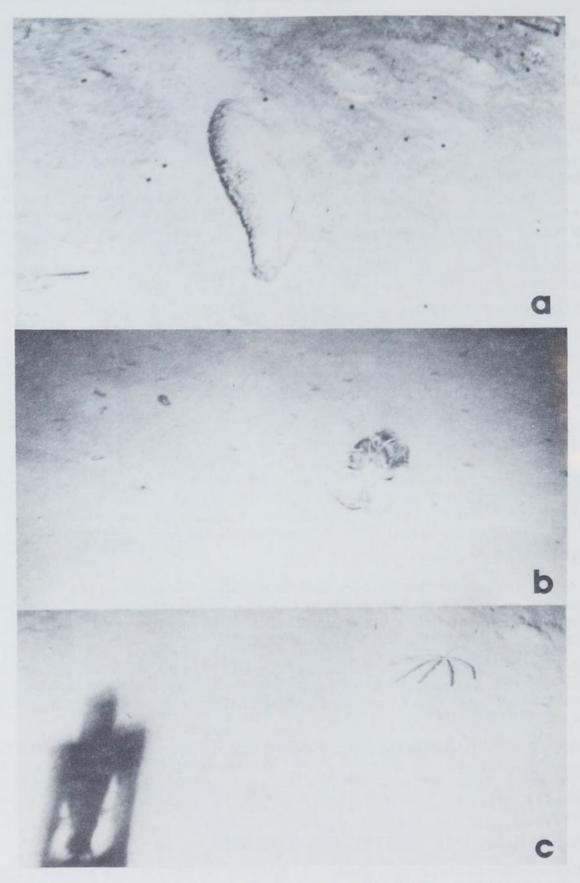


Fig. 5. Holothurian *Pseudostichopus* and asterozoans. 5a, *Pseudostichopus* with covering of sediment and pieces of *Thalassia*. 5b, a specimen of the unidentified "red ophiuroid". 5c the "six-armed *Freyella*" in typical position on the seafloor. This specimen is unusual in having seven arms.

tests for random *versus* non-random distribution patterns, such as were employed by Grassle et al. (1975) in their study of some deep-sea communities. However, it is believed that in spite of the limitations of the data, some inferences can be drawn which would seem to be reasonable in light of the data on feeding propensities presented elsewhere in this paper.

With a few exceptions, population densities were generally rather low. Ophiomusium spp. in transect 2, Benthodytes typica/sanguinolenta in transect 5 and Ellipinion delagei in transect 7 approached densities of 1 per m², but apparently did not exceed them. By contrast, Grassle et al. (1975) found that Ophiomusium lymani in their study area (Dives 280 and 436) was far more numerous, reaching densities of 1.7 and 2.4 specimens per m² respectively. However, densities of other echinoderm species listed by Grassle et al. were relatively low, and tend to agree well with those given here.

a. Distribution patterns of "vegetarians": Hygrosoma petersi, which feeds on Sargassum and Thalassia, was more or less evenly distributed in all transects, except that there was a notable population increase in transect 7 followed by a sharp decline in transect 8. Bathypectinura heros, by contrast, reached relatively high numbers during transects 1-4, and was virtually absent from all subsequent transects except transect 8. Note that the increase in this last transect is matched by a decline in numbers of Hygrosoma petersi.

Although the Sargassum-Thalassia fragments are ubiquitous, it appears that the two species discussed above are not evenly scattered on the seafloor, and that there may be some evidence here of competitive exclusion, involving other species of echinoderms, or other invertebrates.

b. Distribution patterns of "mud-ball swallowers": *Phormosoma placenta* was unevenly distributed over all transects, reaching peaks in transects 1, 2 and 7. *Plesiodiadema antillarum* and *Salenocidaris profundi* were common in the first four transects and then dropped out altogether. Perhaps the latter two species are more selective in their feeding and the endpoint of transect 4 might represent the local southern limit of the "range" of their desirable food resource. No herds of *Phormosoma* like those described by Grassle et al. (1975) were found in the Tongue of the Ocean. Specimens were rather widely scattered.

c. Distribution patterns of "non-selective" mud swallowers: While most deep-sea holothurians might be classed as non-selective in their feeding habits, undoubtedly they continually move to areas of higher nutrient content for their feeding, in the same manner as do their shallow-water counterparts. Table 2 shows that several species are present in relatively low numbers in several transects, and then over a few transects population counts rise dramatically. The two species of *Benthodytes* achieved such high densities in transect 5 that it was impossible to count them with any degree of accuracy. *Ellipinion delagei* reached a peak in transect 7, and by transects 10 and 11 had disappeared completely. *Psychropotes depressa* and *Benthodytes lingua* also reached peak populations in transect 7, but in contrast to *Ellipinion delagei* these species were also well represented in transects 10 and 11.

Paelopatides sp. shows a pattern similar in many respects to that of *Psychropotes depressa* and *Benthodytes lingua*, except that the peaks for the first species were reached in transects 6 and 7, while for the latter two species there was a sharp increase in numbers from transect 6 to transect 7. *Mesothuria verrilli* and *Pseudostichopus* A and B were more or less evenly distributed over all transects, their numbers dropping slowly towards the last transect runs.

Examination of intestine contents of several of the species discussed above revealed no obvious differences at the gross level. A study of organic content of sediments in the various transect areas might be useful. Sanders et al. (1965) found that for the Gay Head — Bermuda study, distribution of animals on the seafloor was not obviously correlated with organic content of the sediment. This negative result was ascribed to an inadequacy in the analytical techniques

used. Clearly, further study of this topic is required.

It is evident from Table 2 that two important population peaks for mud-swallowers were reached in different transects. The first, in transect 7, includes *Ellipinion delagei*, *Psychropotes depressa* and *Benthodytes lingua*, while the second comprises *Benthodytes typica* and *B. sanguinolenta*.

Differing nutritional requirements, competition, aggregation as a result of social behaviour might be suggested as causes for staggering of population peaks for the various feeding categories discussed above. Contagious distributions have been noted in deep-sea echinoderms on several occasions (see Grassle et al., 1975). The phenomenon of social behaviour in echinoderms has received some attention recently (Pearse and Arch, 1969; Grünbaum et al., 1978), and it is possible that the obvious "clumping" of deep-sea species discussed here is the result of some social interaction that is not yet understood. In some cases, the aggregation is clearly related to distribution of food resources, as shown by Pawson (1976) for a species of *Scotoplanes*, but for the most part, no obvious explanations are forthcoming.

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